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Correlating hydrologic reinforcement of vegetated soil with plant traits during establishment of woody perennials

D. Boldrin · Anthony K. Leung · A. G. Bengough

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Abstract

Background and aims Vegetation stabilizes slopes via root mechanical reinforcement and hydrologic reinforcement induced by transpiration. Most studies have focused on mechanical reinforcement and its correlation with plant biomechanical traits. The correlations however generally ignore the effects of hydrologic reinforcement. This study aims to quantify the hydrologic reinforcement associated with ten woody species and identify correlations with relevant plant traits.

Methods Ten species widespread in Europe, which belong to Aquifoliaceae, Betulaceae, Buxaceae, Celastraceae, Fabaceae, Oleaceae and Salicaceae families, were planted in pots of sandy loam soil. Each planted pot was irrigated and then left to transpire. Soil strength, matric suction and plant traits were measured.

Results Transpiration-induced suction was linearly correlated with soil penetration resistance for the ten species due to their different transpiration rates i.e. both suction and soil penetration resistance induced by Hazel and Blackthorn (deciduous) were five times greater than

those by Holly and European Box (evergreens). Specific leaf area and root length density correlated with hydrologic reinforcement. The root:shoot ratio correlated best with the hydrologic reinforcement.

Conclusions Specific leaf area, root length density and root:shoot ratio explained the tenfold differences in hydrologic reinforcement provided by the ten different species.

Keywords Hydrologic reinforcement · Matric suction · Soil bioengineering · Soil strength · Transpiration

Introduction

Soil bioengineering using vegetation is an environmentally-friendly technique for not only shallow slope stabilisation, but also creating sustainable ecosystems within the built environment (Stokes et al. 2008; Stokes et al. 2014). Vegetation is known to provide slope stabilisation via mechanical reinforcement through root anchorage (Mickovski et al. 2009; Ghestem et al. 2014b; Kamchoom et al. 2014; Meijer et al. 2016). Change in soil shear strength due to transpiration-induced matric suction (known as hydrologic reinforcement) is also increasingly recognised to be important for slope hydrology and stability (Lim et al. 1996; Simon and Collison 2002; Pollen-Bankhead and Simon 2010; Smethurst et al. 2012; Leung and Ng 2013; Garg et al. 2015; Ng et al. 2015; Smethurst et al. 2015). Extensive field and laboratory studies have shown that transpiration-

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induced suction could be maintained in the soil during and after rainfall (Ng et al. 2013; Ng et al. 2014; Rahardjo et al. 2014; Leung et al. 2015a; Ng et al. *in press*). Recent research also argues that the presence of roots could affect the soil water retention properties and hence the suction responses (Bengough 2012; Carminati and Vetterlein 2013; Scholl et al. 2014; Leung et al. 2015b; Ng et al. 2016a, 2016b). The ability of plants to preserve/maintain suction has important implications for slope stability. A field study conducted by Rahardjo et al. (2014) showed that slopes covered with shrub and grass species were able to preserve significant suction even after 24 h of rainfall, resulting in a drop of factor of safety (~6% decrease in factor of safety, FOS) much less than found in a fallow slope (25.9% decrease in FOS) where no suction was preserved. Several recent studies have identified that hydrologic reinforcement can have greater effects on soil stabilisation than mechanical reinforcement by root inclusions (Simon and Collison 2002; Pollen-Bankhead and Simon 2010). In particular, Veylon et al. (2015) showed that hydrologic reinforcement contributed up to 80% of soil shear strength. These studies have highlighted the hydrologic reinforcement via soil-plant interactions. Yet, more evidence is needed to examine such phenomena and reveal the underlying mechanisms.

There has been an increasing focus in using plant traits as screening criteria to assist engineers to identify suitable species for slope stabilisation (Stokes et al. 2009). A plant trait is defined as a distinct and quantitative feature of a species in terms of plant morphology, physiology or biomechanics (Pérez-Harguindeguy et al. 2013). For mechanical reinforcement, biomechanical traits, such as root tensile strength and root architecture, are found to influence the shear strength of root-permeated soils (Mattia et al. 2005; De Baets et al. 2008; De Baets et al. 2009; Stokes et al. 2009; Ghestem et al. 2014b). There is little information about plant traits affecting hydrologic reinforcement. To-date, only a few studies have attempted to associate plant traits with hydrologic reinforcement (Saifuddin and Osman 2014; Ng et al. 2016a, b) for species native to Asia. However, the number of plant traits and species being tested are very small in comparison with the many possible traits and species combinations. Determining the hydrologic reinforcement of vegetation requires knowledge of actual transpiration rate, which is difficult to assess in the field. Engineers who would want to apply soil bioengineering technique need

to identify relevant plant traits for plant screening and selection in relation to the hydrologic reinforcement of candidate species.

The objective of this study is to quantify and compare the hydrologic reinforcement induced by ten selected woody species widespread in Europe and to associate such reinforcement with functional traits corresponding to hydrological strategies and morphological characteristics. We hypothesize that (i) these woody species transpire and induce contrasting soil suctions during the early establishment period and (ii) plant traits (both above- and below-ground) are associated with hydrologic reinforcement.

Methods

Selected plant species

Ten woody species, which would grow into shrubs or small trees, were selected for testing in this study. Species chosen were *Buxus sempervirens* L.; *Corylus avellana* L.; *Crataegus monogyna* Jacq.; *Cytisus scoparius* (L.) Link; *Euonymus europaeus* L.; *Ilex aquifolium* L.; *Ligustrum vulgare* L.; *Prunus spinosa* L.; *Salix viminalis* L. and *Ulex europaeus* L. Their family, common name, functional type and the acronym used throughout this study are summarised in Table 1. These species were selected due to wide spread populations in Europe, and relatively high adaptability to a wide range of environmental conditions. Most of these species are within the Trunk Road Biodiversity Action Plan recommended by the Scottish Government for enhancing the ecological values and landscape of roadside slopes/embankments (see online document 1). Moreover, these species have been suggested as suitable plants for soil bioengineering and eco-technological solutions in the European context (Coppin and Richards 1990; Marriott et al. 2001; Norris et al. 2008; Beikircher et al. 2010). In particular, *C. avellana* and *S. viminalis* are found to be highly suitable for slope stabilisation through mechanical reinforcement (Bischetti et al. 2005; Mickovski et al. 2009).

Soil and planted pots

The soil investigated in this study was collected from Bullionfield, The James Hutton Institute, Dundee, UK. It was a sandy loam, which comprised of 71% sand, 19% silt and 10% clay contents (Loades et al. 2013).

Table 1 A list of the ten species selected for testing in this study. Their family, common name, functional type and the acronym used throughout this study are reported

Species	Family	Common name	Functional type	Acronym
<i>Buxus sempervirens</i> L.	Buxaceae	European Box	evergreen	Bs
<i>Corylus avellana</i> L.	Betulaceae	Hazel	deciduous	Ca
<i>Crataegus monogyna</i> Jacq.	Rosaceae	Hawthorn	deciduous	Cm
<i>Cytisus scoparius</i> (L.) Link	Fabaceae	Scotch broom	evergreen	Cs
<i>Euonymus europaeus</i> L.	Celastraceae	Spindle	deciduous	Ee
<i>Ilex aquifolium</i> L.	Aquifoliaceae	Holly	evergreen	Ia
<i>Ligustrum vulgare</i> L.	Oleaceae	Privet	deciduous	Lv
<i>Prunus spinosa</i> L.	Rosaceae	Blackthorn	deciduous	Ps
<i>Salix viminalis</i> L.*	Salicaceae	Willow	deciduous	Sv
<i>Ulex europaeus</i> L.	Fabaceae	Gorse	evergreen	Ue

*indicates the propagation by cutting. All plants were supplied by British Hardwood Tree Nursery, Gainsborough, UK

The liquid limit of the soil was 32%, while the plastic limit was 23%. The soil (sieved <10 mm; water content 0.15 g/g) was dynamically compacted in five layers in pots (0.24 m in diameter and 0.009 m³ in volume) to obtain an initial dry density of 1200 kg m⁻³. This dry density was used to favour fast root growth and development during plant establishment (Loades et al. 2013). During compaction, the surface of each layer was abraded to achieve a better contact between each successive layer. After packing the fourth layer, a bare root plant was transplanted into the pot and then the fifth layer was packed carefully around the root system. Five replicates of each species were prepared giving a total of 50 planted pots. The top soil surface of the pot was covered with a 10 mm-thick gravel layer to minimize soil evaporation. All planted pots were randomly arranged on benches in a glasshouse (9 pots per m²; average daily temperature 18 ± 5 °C and daily relative humidity between 50% – 80%). Pots were watered to field capacity twice weekly for two months to encourage plant establishment. The plants were considered established when canopies were expanding stably and appropriately for each species. In addition to planted pots, three control, fallow, pots were prepared, covered with a thin gravel layer and subjected to the identical irrigation schedule as planted pots. Due to the irrigation and wetting-drying processes, soil bulk density changed with time (Horn 2004). The dry density found at the end of the tests was about 1500 kg m⁻³.

The soil water retention curve (SWRC) was obtained from three replicated cores (55 mm in diameter; 40 mm in height) of fallow sandy loam, compacted at the dry density of 1200 kg m⁻³. Each core was subjected to

suctions ranging from 1 to 1500 kPa using a tension Table (1–50 kPa) and a pressure plate apparatus (50–1500 kPa; ELE International, Hemel Hempstead, UK). The SWRC was fitted by the equation proposed by van Genuchten (1980). Note that here we express water content in gravimetric term not volumetric:

$$w = w_r + \frac{w_s - w_r}{[1 + |\alpha\Psi|^n]^m}$$

where w is the soil water content (gg⁻¹), w_r is the residual soil water content at 1500 kPa (gg⁻¹), w_s is the saturated soil water content (gg⁻¹), Ψ is soil matric suction (kPa), α , n , and m are parameters that describe the shape of the curve, $m = 1 - 1/n$, $0 < m < 1$.

Measurements of plant transpiration and soil suction

After initial plant establishment, all 50 planted pots and the three fallow pots were irrigated until the soil was close to saturation, as indicated by a 0 kPa of matric suction recorded by a miniature tensiometer (SWT-5, Delta-T devices, Cambridge, UK) that was horizontally installed approximately in the middle of each pot (120 mm from soil surface; 80 mm from pot side). Each pot was then left in the glasshouse for evapotranspiration (ET, planted pots) and evaporation (E, fallow pots) for 13 days. All pots were weighed daily on a balance (ExplorerPro, Ohaus, Switzerland) with an accuracy of 0.1 g to monitor water loss. Measured daily water loss was assumed equal to the daily ET in planted pots and the daily E in fallow pots. Daily transpiration

(T) of each planted pot was estimated from the difference between ET and E in the period between day 2 and 9. Matric suction was recorded in all three fallow pots and three of the replicated plant pots for each species using a tensiometer on the seventh day of monitoring, when most of the planted pots have a large and evident water loss.

Soil penetration resistance

Soil penetration resistance tests (MPa; Weaich et al. 1992) were carried out in each pot using a portable penetrometer (Basic Force Gauge, Mecmesin, UK; cone diameter of 2.96 mm and cone angle of 30°) to quantify the hydrologic reinforcement in the soil due to transpiration-induced suction. Soil resistance was determined by penetrating the cone to 35 mm depth from the soil surface. The small cone diameter and shallow penetration depth were chosen to avoid the effect of soil confinement due to pot size (Misra and Li 1996). The measurements were taken at three different points for each replicate on the seventh day of monitoring (i.e., following the matric suction measurement). Compared to other techniques for quantifying soil strength measurements, such as shear boxes, the major advantage of penetration testing was that the hydrologic reinforcement due to transpiration-induced suction can be mostly isolated from the mechanical reinforcement of roots. The use of a penetrometer offers a relatively quick and less destructive way to determine soil strength. Due to the simplicity of the testing method, multiple penetration tests can be carried out using the same pot, hence reducing the variability of test results. Soil penetration resistance has been used as a parameter to indicate the mechanical or hydrologic reinforcement effects of vegetation on slopes by Osman and Barakbah (2006, 2011). Previous studies showed that the soil penetration resistance correlates with shear strength (Bachmann et al. 2006; Rémai 2013).

Measurement of morphological and architectural traits

A number of plant traits were measured to help understand the hydrologic reinforcement induced by the ten different species. The above-ground traits included specific leaf area (SLA; $\text{m}^2 \text{kg}^{-1}$), wood and leaf biomass (g), green mass ratio (the ratio between green biomass and the total above-ground biomass; g g^{-1}), plant height (cm) and wood density (main stem; g cm^{-3}). Below-

ground traits included specific root length (SRL; m g^{-1}), root biomass (g), total root length (m), root length density (RLD; cm cm^{-3}) and root:shoot ratio (the ratio between below-ground and above-ground biomass; g g^{-1}). All plant traits were measured according to the standardized methodology proposed by Pérez-Harguindeguy et al. (2013).

Specific leaf area (SLA) is defined as the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $\text{m}^2 \text{kg}^{-1}$. SLA was measured for all ten species at the end of the establishment period. Ten fully expanded leaves per species were collected at the beginning of the day when plants would be at maximum hydration. Leaves were scanned and surface area was measured by using the analysis software, ImageJ (NIH, USA). Following the measurement, each leaf sample was oven-dried at 60 °C for 72 h until a constant weight was measured by an electronic 4-decimal-place balance. SLA was calculated by dividing the leaf area by the corresponding leaf dry weight.

After 13 days of monitoring, leaf and wood biomass (i.e., green and non-green biomass) of each species were measured by oven-drying the plant material at 60 °C until a constant weight was obtained. It should be noted that for *C. scoparius* and *U. europaeus* it was not possible to separate green and non-green biomasses due to the presence of partially green shoots and thorns. Therefore, only the total above-ground biomass was measured.

After testing, roots of each species were washed from soil using a set of sieves (from 2 mm to 0.5 mm mesh). Representative subsamples of the root system (an average 10% of root system by weight) were scanned and analysed using WinRhizo (Regent Instruments Inc.) to determine root length. Measured length and dry mass of root subsamples were used to obtain the specific root length (SRL, root length by mass). The entire root system of each species was oven-dried at 60 °C to determine root biomass. The total root length in each planted pot was then estimated by multiplying the dry root biomass by the SRL. Thick roots (>5 mm diameter), if present, were processed and analysed separately to avoid overestimation of root length. Root length density (RLD) was obtained by dividing the total root length by the soil volume in the pots (0.008 m^3).

Leaf conductance to water vapor

Leaf conductance to water vapor (g_L ; $\text{mmol m}^{-2} \text{s}^{-1}$) was measured on at least one leaf for all replicates using a

portable porometer (AP4, Delta-T devices, Cambridge, UK). This device is a dynamic diffusion porometer in which part of the leaf is enclosed at the base of a cup containing a humidity sensor. Dry air is then flushed through the cup until a pre-selected drier relative humidity is achieved. The flushing then stops and the transit time required for a small, fixed increase in relative humidity is measured. The time taken for the humidity to increase over the fixed interval is related to g_L via a calibration curve. Before measurement, the porometer was calibrated using a perforated plate with known diffusive conductance to water vapor. The theoretical basis of a dynamic diffusion porometer is described by Monteith et al. (1988). Measurements of g_L were made on a sunny day, when all the planted pots showed an evident and stable water loss.

Statistical analysis

Statistical analysis was performed using GenStat 17th Edition (VSN International) and SigmaPlot13 (Systat Software Inc). Significant differences were assessed with one way-ANOVA, followed by post hoc Tukey's test. The significance of correlations established in this study was tested using regression analysis. Results were considered statistically significant when p -value ≤ 0.05 . Principal-component analysis was conducted to examine the relationships among traits and between traits and soil parameters.

Results

Soil water retention curve

The soil water retention curve of the sandy loam showed a fast decrease of water content in matric suction range between 1 and 5 kPa (Fig. 1). The amount of water available to plants (Kirkham 2005), which was calculated by the difference between water content (WC) at field capacity (i.e., 5 kPa suction, Townend et al. (2000) and WC at the permanent wilting point (i.e., 1500 kPa suction), was equal to 0.14 g g^{-1} .

Plant-soil water relations

The total water loss in all planted pots ($>2.5 \text{ g}$ per 100 g of soil) was always higher than that in the fallow pots ($195.9 \pm 13.3 \text{ g}$ of water per pot $\approx 2.0 \text{ g}$ per 100 g

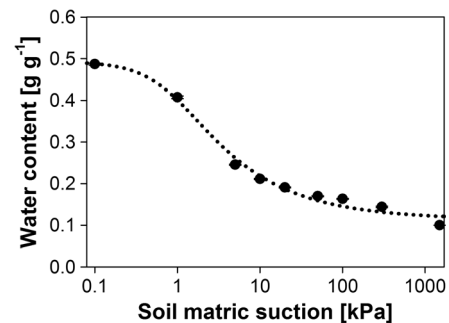


Fig. 1 Soil water retention curve of Bullionfield soil sieved to 10 mm and compacted to dry density of 1200 kg m^{-3} . Mean values of three replicates (\pm Standard error of mean, though smaller than symbol dimensions) are used in curve fitting for the van Genuchten (1980) model [$w_s = 0.49$; $w_r = 0.11$; $\alpha = 1.16$; $n = 1.52$; $R^2 = 0.99$]

of soil; Fig. 2). Three distinct patterns of water uptake can be identified from the figure. The species, *B. sempervirens* and *I. aquifolium*, have the lowest water uptake, resulting in a final water loss of less than 5 g per 100 g of soil ($\approx 500 \text{ g}$ of water per pot). Water loss of more than 15 g per 100 g dry soil ($\approx 1500 \text{ g}$ of water per pot) was found for the species, *C. scoparius* and *U. europaeus*, which showed the greatest water uptake. The remaining six species showed intermediate water uptake, removing soil moisture in a range between 10 g per 100 g dry soil ($\approx 1000 \text{ g}$ of water per pot) and 15 g per 100 g dry soil ($\approx 1500 \text{ g}$ of water per pot).

The estimated daily transpiration was correlated with matric suction measured at the seventh day of

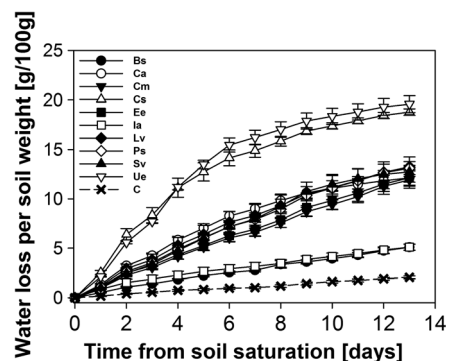


Fig. 2 Measured water loss from planted and fallow pots during 13-day of monitoring period normalized by dry soil weight. Dashed line represents water loss in fallow pots (C). Error bars represent \pm the standard error of mean ($n = 5$). Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*)

monitoring in each planted pot (Fig. 3). The regression analysis highlights a significant linear correlation between them. Smallest values of suction (2.84 ± 0.44 kPa) were recorded in *I. aquifolium* pots, whereas *U. europaeus* induced the greatest suction (75.19 ± 5.37 kPa).

A linear correlation between the seventh-day matrix suction and penetration resistance (Fig. 4) highlighted the hydrologic reinforcement induced by plant transpiration. Compared with the fallow pots, the penetration resistance in the planted pots was always greater. Plants with large water uptake, such as *C. scoparius* and *U. europaeus*, gained the most soil penetrometer resistance, which was 11 and 10 times larger than that in control, fallow soil, respectively. These species showed different degrees of hydrologic reinforcement due to the differences in their transpiration rates (Figs 2 and 3).

Correlations between plant traits and hydrologic reinforcement

The main above- and below-ground traits showed significant differences among species (Table 2). A principal-component (PC) biplot (Fig. 5) shows that from the projection of plant traits and soil hydro-mechanical characteristics on the plane composed by the two first explanatory axes (PC1: 48% of variation; PC2: 24% of variation), three major groups of plant traits can be defined. The first PC axis is positively correlated with traits associated with soil hydro-

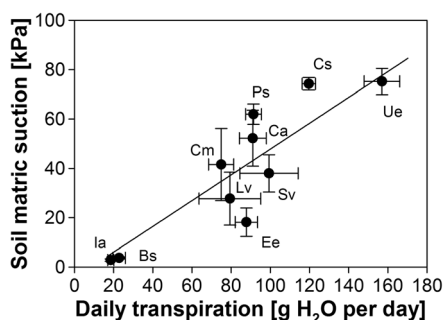


Fig. 3 Relationship between daily transpiration and matrix suction. Mean values of species are reported \pm standard error of mean ($n = 3$). Linear regression of all data points from all replicates (non-average values) is given [$f = -4.4156 + 0.5227 \cdot x$; P -value < 0.0001 ; $R^2 = 0.58$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*)

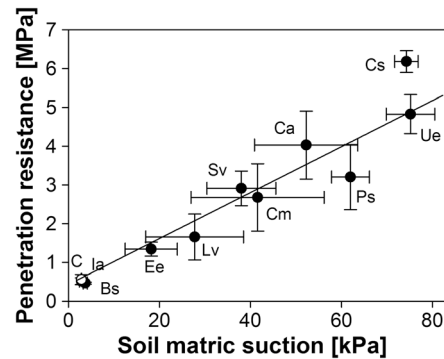


Fig. 4 Relationship between matrix suction and soil penetration resistance in planted and fallow pots (C; open symbol). Mean values of species are reported \pm standard error of mean ($n = 3$). Linear regression of all data points from all replicates (non-average values) is given [$f = 0.4317 + 0.0593 \cdot x$; P -value < 0.0001 ; $R^2 = 0.73$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*)

mechanical characteristics (i.e., matrix suction and penetration resistance) such as specific leaf area, root length density and root:shoot ratio. On the other hand, the second PC axis is related positively with plant traits associated with plant hydraulic conductivity (i.e., leaf conductance; specific root length (Eissenstat 1992; Rieger and Litvin 1999) and negatively related with traits associated with plant size (plant height; shoot biomass; root biomass and total biomass). The small angles between soil hydro-mechanical characteristics and plant traits indicate that biomass allocation and investment (specific leaf area; root length density; root:shoot ratio) have strong correlations among these parameters. On the contrary, plant traits associated with plant size were not correlated with soil hydro-mechanical characteristics (wide angles). Leaf conductance, specific root length and transpiration efficiency (transpiration per shoot biomass, g g^{-1}) were positively related each other but negatively related with wood density.

Total biomass (wood, leaf and root biomass) differed greatly amongst species, ranging from 16.8 ± 1.52 (*I. aquifolium* pots) to 191.5 ± 7.3 g (*C. scoparius* pots). However, neither the PC biplot nor the regression analysis shows any correlation between hydrologic reinforcement characteristics (matrix suction and penetration resistance) and biomass (Fig. 5 and supplementary Figs 3, 4 and 5). Transpiration efficiency of a species was estimated by dividing the daily transpiration by the above-ground (i.e., leaf and wood) biomass (Fig. 6).

Table 2 Main above and below-ground traits of each species (mean \pm standard error of mean)

Species	Wood biomass, g	Leaf biomass, g	Specific leaf area, m ² kg ⁻¹	Leaf conductance to water vapor, mmolm ⁻² s ⁻¹	Root biomass, g	Specific root length, m g ⁻¹
<i>Buxus sempervirens</i> (Bs)	12.79 \pm 1.99	13.02 \pm 2.87	8.55 \pm 1.53b	44.30 \pm 9.9a	7.4 \pm 1.0	18.84 \pm 1.14a
<i>Corylus avellana</i> (Ca)	28.88 \pm 2.92	12.46 \pm 1.24	22.01 \pm 1.09d	55.24 \pm 8.7abc	29.7 \pm 3.1	21.10 \pm 1.88ab
<i>Crataegus monogyna</i> (Cm)	18.34 \pm 2.48	7.16 \pm 0.63	15.98 \pm 0.42c	140.80 \pm 20.4bcd	15.0 \pm 0.9	26.31 \pm 6.07ab
<i>Cytisus scoparius</i> (Cs)	162.1 \pm 9.9	-	-	26.52 \pm 7.9a	16.8 \pm 0.7	28.47 \pm 2.57ab
<i>Euonymus europaeus</i> (Ee)	38.03 \pm 5.66	14.92 \pm 1.46	17.92 \pm 0.38c	49.98 \pm 10.2ab	23.9 \pm 6.1	18.65 \pm 0.86a
<i>Ilex aquifolium</i> (Ia)	6.39 \pm 0.49	8.00 \pm 0.90	4.27 \pm 0.24a	26.64 \pm 5.7a	2.4 \pm 0.3	28.68 \pm 3.70ab
<i>Ligustrum vulgare</i> (Lv)	29.35 \pm 3.17	14.28 \pm 2.48	14.56 \pm 0.88c	63.30 \pm 14.6abc	22.0 \pm 4.1	15.55 \pm 1.16a
<i>Prunus spinosa</i> (Ps)	13.65 \pm 1.37	6.65 \pm 1.09	23.44 \pm 0.86d	153.20 \pm 17.4 cd	15.5 \pm 0.9	36.23 \pm 5.31bc
<i>Salix viminalis</i> (Sv)	25.09 \pm 4.40	2.94 \pm 0.21	21.88 \pm 0.44d	417.60 \pm 124.4d	15.9 \pm 1.1	64.52 \pm 9.03c
<i>Ulex europaeus</i> (Ue)	68.80 \pm 4.34	-	-	56.40 \pm 8.4abc	12.7 \pm 1.3	28.91 \pm 1.62ab

Letters in SLA, g_L and SRL columns indicate significant differences among species, as tested using one-way ANOVA followed by post hoc Tukey's test (g_L and SRL data were log transformed). Total biomass (wood, leaf and root biomass) among species showed significant differences (P -values < 0.001, one-way ANOVA of log transformed data)

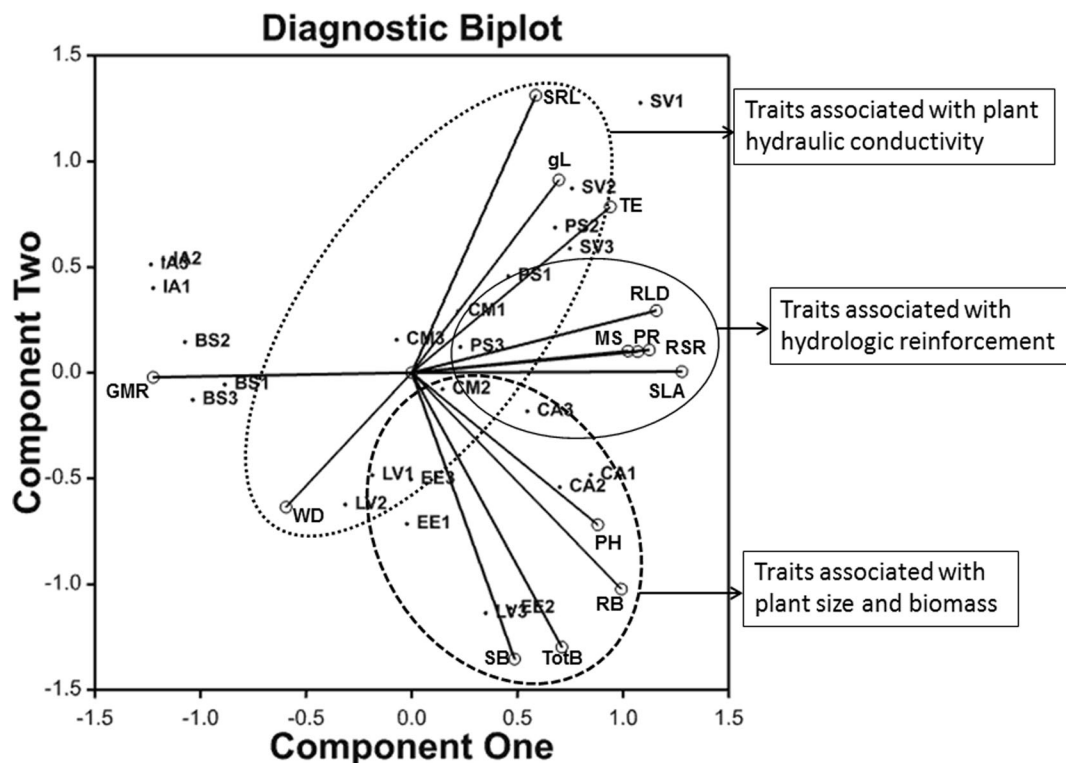


Fig. 5 Biplot projection of plant traits and soil hydro-mechanical parameters on the plane represented by the first two components of principal component (PC) analysis (PC1: 48% of variation; PC2: 24% of variation). Acronyms of plant traits and soil parameters: g_L (leaf conductance); GMR (green mass ratio); MS (Matric suction); PH (plant height); PR (penetration resistance); RB (root biomass); RLD (root length density); RSR (root:shoot ratio); SB (shoot biomass); SLA (specific leaf area); SRL (specific root length);

TE (transpiration efficiency); Tot B (total biomass); WD (wood density). Species acronyms: BS (*Buxus sempervirens*); CA (*Corylus avellana*); CM (*Crataegus monogyna*); EE (*Euonymus europaeus*); IA (*Ilex aquifolium*); LV (*Ligustrum vulgare*); PS (*Prunus spinosa*) and SV (*Salix viminalis*). Three replicates per each species. *Cytisus scoparius* and *Ulex europaeus* were not included in the principal component analysis due to the missing values in leaf related traits

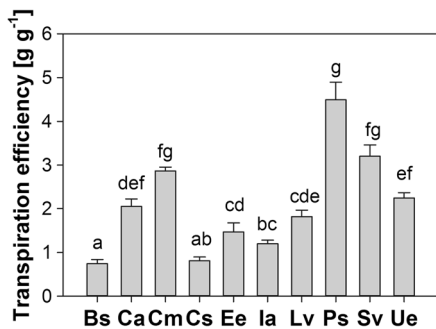


Fig. 6 Transpiration efficiency (normalised daily transpiration per above-ground biomass). Means are reported \pm standard error of mean ($n = 5$). Letters indicate significant differences among species, as tested using one-way ANOVA followed by post hoc Tukey's test (data were log transformed). Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*)

P. spinosa showed the highest efficiency with 4 g of transpired water per each g of dry biomass. *C. scoparius* was least efficient ($< 1 \text{ g g}^{-1}$), low transpiration compared to the above-ground biomass (Fig. 6; Table 2). Therefore, the high ET values recorded in *C. scoparius* pots (Fig. 2) can be mainly explained by their large above-ground biomass.

Transpiration efficiency was positively correlated with g_L , as highlighted by both the PC biplot (Fig. 5) and the regression analysis (Fig. 7). Note that *S. viminalis* is not considered in this correlation (Fig. 7) because although this species has both high g_L and transpiration efficiency, they were not related as in the other nine species, due to its outstanding g_L . The high g_L values of *S. viminalis*

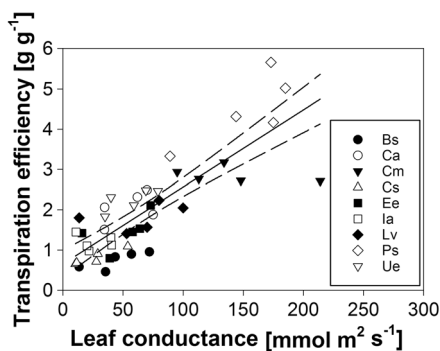


Fig. 7 Relationship between leaf conductance to water vapor (g_L) and transpiration efficiency (daily transpiration per above-ground biomass) [$f = 0.6546 + 0.0191 \cdot x$; P -value < 0.0001 ; $R^2 = 0.67$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*) and Ue (*Ulex europaeus*)

(Table 2) reflects its adaptation to wet habitats (Korner et al. 1979).

Both transpiration efficiency and leaf conductance highlighted a significant difference between deciduous and evergreen species (Fig. 8). Indeed, the transpiration efficiency (Fig. 8a) and leaf conductance (Fig. 8b) of deciduous species were more than two times greater than those of evergreen species.

There was significant difference in SLA among the ten species (Table 2). Generally, deciduous species had three times higher average SLA ($19.1 \pm 0.48 \text{ m}^2 \text{ kg}^{-1}$) than evergreen ($6.6 \pm 0.65 \text{ m}^2 \text{ kg}^{-1}$). The differences were attributable to probably the thicker and stiffer

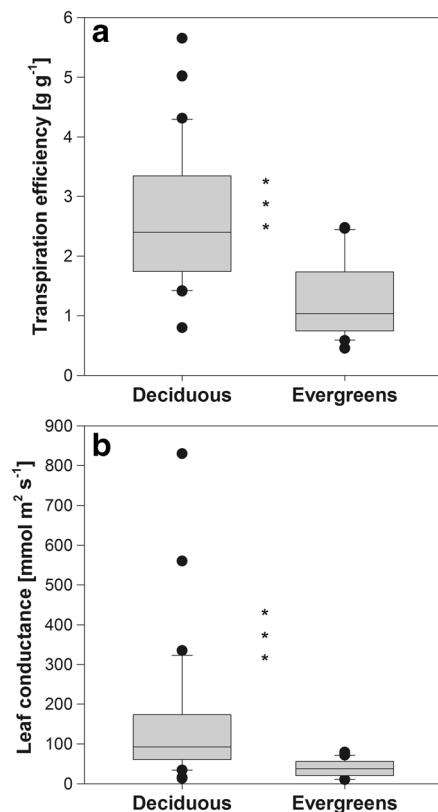


Fig. 8 Box plots of transpiration efficiency (A) and leaf conductance (B) in deciduous and evergreen species. Deciduous species ($n = 30$): Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Ee (*Euonymus europaeus*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*). Evergreen species ($n = 20$): Bs (*Buxus sempervirens*); Cs (*Cytisus scoparius*); Ia (*Ilex aquifolium*) and Ue (*Ulex europaeus*). The bottom and top of boxes represent the 25th and 75th percentile, while the line within the box marks the median. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Black circles are outlying points. Leaf conductance data were log transformed in the statistical analysis (one-way ANOVA). *** represents a significant difference (P -values < 0.001)

leaves of the evergreen species. SLA was positively correlated with both matric suction (Fig. 9a) and soil penetration resistance (Fig. 9b).

The RLD of the ten species ranged between 1.1 cm cm^{-3} and 8.4 cm cm^{-3} , which was consistent with the range found in field top soils with large root length density (Stokes 1999; Gregory, 2008 RLD was significantly and linearly correlated with both matric suction (Fig. 10a) and soil penetration resistance (Fig. 10b), when the results obtained from *S. viminalis* were not included. The contrasting behaviour of *S. viminalis* may be explained by its cutting origin. Out of the ten tested species, *S. viminalis* was the only one that was grown from a stem cutting, which can result in rather different shoot and root morphologies (Bryant and Trueman 2015).

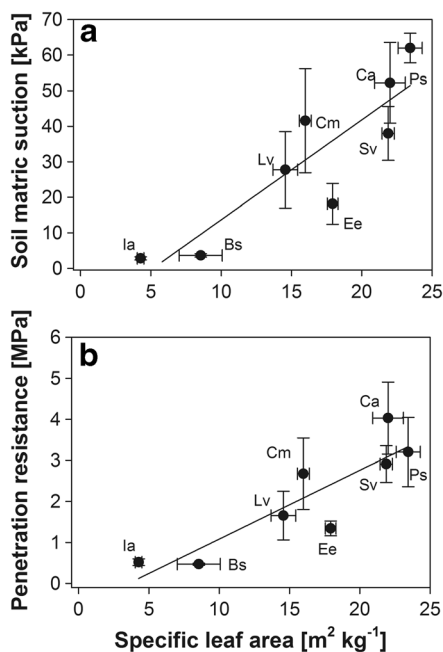


Fig. 9 Relationship of SLA with matric suction (A) and soil penetration resistance (B) in planted pots. Mean values of species are reported \pm standard error of mean ($n = 3$ for soil parameters; $n = 10$ for SLA). Linear regressions of all data points from all replicates (non-average values) are given [(A) $f = -14.4182 + 2.8112 \cdot x$; P -value < 0.0001 ; $R^2 = 0.56$; (B) $f = -0.5932 + 0.1676 \cdot x$; P -value < 0.0001 ; $R^2 = 0.50$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*) and Sv (*Salix viminalis*). It should be noted that *C. scoparius* and *U. europaeus* were not considered in the regression analyses due to the absence of leaves (*U. europaeus*) or their limited number and dimension (*C. scoparius*) compared with green twigs and thorns, which are the main photosynthetic organs in these species

Root:shoot ratio was significantly correlated with matric suction (Fig. 11a) and soil penetration resistance (Fig. 11b). Compared to other traits, root:shoot ratio provided the best correlation with hydrologic reinforcement developed by transpiration-induced suction.

Discussion

The test results showed substantial differences among the ten species in terms of water uptake (Fig. 2) and its effects on induced suction (Fig. 3). It is clear that different species induced different degree of hydrologic reinforcement (Fig. 4), and this depended primarily on their rate of water uptake, which was significantly affected by the plant traits (Figs 5, 9, 10 and 11).

It has been generally recognised that plant water uptake is affected by biomass (both above- and below-ground) as well as physiological factors (Lambers et al. 2008; Osman and Barakbah 2011; Jones 2013). Interestingly, the PC biplot (Fig. 5) shows that biomass allocation (e.g. root:shoot ratio) and biomass investment such as leaf surface (e.g. specific leaf area) and root length (e.g. root length density) were strongly and positively correlated with hydrologic reinforcement (i.e., matric suction and penetration resistance). However, plant size and biomass were not correlated with both matric suction and penetration resistance, when the ten different species were considered (Figs 5 and 6; supplementary Figs 3, 4 and 5). The lack of correlation between biomass and water uptake in our experiment was also highlighted by the significantly different transpiration efficiency among species (Fig. 6). Transpiration efficiency can be particularly relevant in species selection for soil hydrologic reinforcement. It is thus crucial to isolate the effects of biomass when estimating the effects of species on water uptake ability, so that the estimation is not biased by the plant dimension.

This highlighted that other physiological factors differing among species, such as leaf conductance to water vapor, could have considerable effect on transpiration and transpiration efficiency, limiting the expected effects of biomass. In fact, transpiration efficiency correlated with leaf conductance (g_L ; Fig. 7). For species such as *P. spinosa*, the high g_L may be one of the key factors that compensated for the low biomass and induced the relatively high suction.

Leaf conductance varied with plant functional groups, with the lowest values recorded in succulents

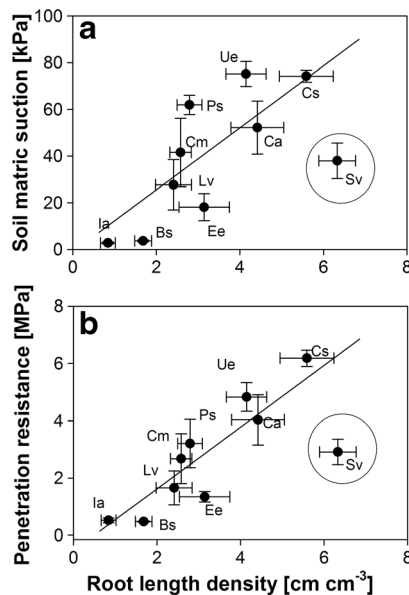


Fig. 10 Relationship of RLD with matric suction (A) and soil penetration resistance (B) in planted pots. Mean values of species are reported \pm standard error of mean ($n = 3$). Linear regressions of all data points from all replicates (non-average values) are given [(A) $f = -0.9510 + 13.2804 \cdot x$; P -value < 0.0001 ; $R^2 = 0.47$; (B) $f = -0.5373 + 1.0787 \cdot x$; P -value < 0.0001 ; $R^2 = 0.63$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*). *S. viminalis* was not included in regression analysis. Note that this species was grown from cutting whilst all other species were grown from seeds

and the highest values in plant of wet habitats such as *S. viminalis* (Komer et al. 1979). Changes in stomatal opening, and hence leaf conductance to water vapor, can strongly affect root-water uptake and hence the soil water balance (Hungate et al. 2002; Gedney et al. 2006; Betts et al. 2007). Hussain et al. (2013) showed that a decrease in leaf conductance of Maize caused a reduction of soil water depletion by 5% – 10%. Simple measurements of leaf conductance using a portable porometer could provide a quick assessment of transpiration of a plant. It should, however, be noted that any use of leaf conductance as a plant screening parameter is meaningful only in the absence of water stress, as water stress rapidly decreases leaf conductance to water vapor by closing stomata (Hsiao 1973).

Transpiration efficiency and leaf conductance also highlighted a significant difference between deciduous and evergreen species, with deciduous species twice as efficient in removing soil water as evergreens (Fig. 8). Indeed, in cold temperate climates deciduous species

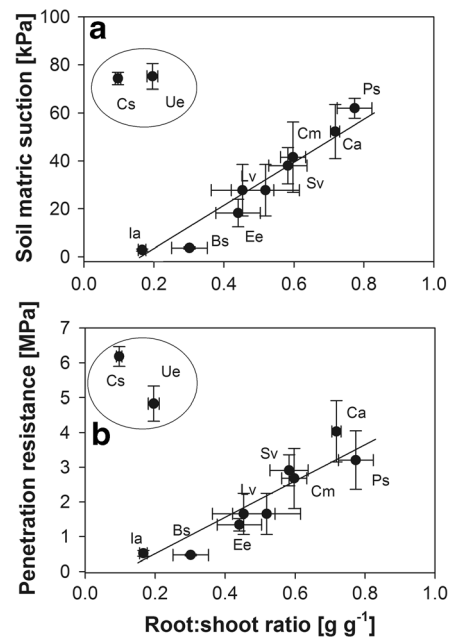


Fig. 11 Relationship of root:shoot ratio with matric suction (A) and soil penetration resistance (B) in planted pots. Mean values of species are reported \pm standard error of mean ($n = 3$). Linear regressions of all data points from all replicates (non-average values) are given [(A) $f = -17.0648 + 93.3896 \cdot x$; P -value < 0.0001 ; $R^2 = 0.65$; (B) $f = -0.6501 + 5.3716 \cdot x$; P -value < 0.0001 ; $R^2 = 0.54$]. Species acronyms: Bs (*Buxus sempervirens*); Ca (*Corylus avellana*); Cm (*Crataegus monogyna*); Cs (*Cytisus scoparius*); Ee (*Euonymus europaeus*); Ia (*Ilex aquifolium*); Lv (*Ligustrum vulgare*); Ps (*Prunus spinosa*); Sv (*Salix viminalis*) and Ue (*Ulex europaeus*). *C. scoparius* and *U. europaeus* were not included in regression analysis. Note that photosynthetic organs of these two species are mainly constituted by photosynthetic leaves, twigs and thorns whilst the other species have only leaves

have to maximize their growth and hence the water uptake during a short growing season (summer) whilst evergreen species have a longer growing season and hence a slow-return of energy investment and small water use (Wright et al. 2004). Moreover, evergreen trees are generally known to have smaller hydraulic conductance than deciduous trees (Tyree and Cochard 1996). Martínez-Vilalta et al. (2002) showed that hydraulic properties of *I. aquifolium*, such as small conduit diameters and hence low xylem conductance, are related to avoidance of freezing-induced xylem embolism in the cold areas where this species normally lives. On the contrary, the evergreen *C. scoparius* may be considered as a summer drought avoider, shedding its leaves during summer drought to reduce transpiration while maintaining stem photosynthetic function (Matias et al. 2012). Both these strategies, enhancing hydraulic safety and

water saving, may explain the low transpiration efficiency exhibited by both *C. scoparius* and *I. aquifolium* (Fig. 6).

The PC biplot (Fig. 5) shows strong correlations between hydrologic reinforcement and some plant traits (specific leaf area, root length density and shoot:root ratio), which may thus be used to identify the relative transpiration-induced suction from different species, and the associated gain in soil strength.

For the above-ground traits, the specific leaf area (SLA) showed a positive linear correlation with the hydrologic reinforcement (Fig. 9). Hence, it was not the leaf biomass that controlled the hydrologic reinforcement, but rather its allocation and investment such as leaf surface area. SLA is an indicator of energy strategy and adaptation to environment of a species. SLA of the selected deciduous species was higher than that of the selected evergreens (Table 2), consistent with the data reported by Poorter et al. (2009) and the observed difference in terms of transpiration efficiency of the two functional types (Fig. 8). The observed differences in SLA among the ten species were attributable to the different spectrum of leaf economics, which reflected the plant investment in leaf tissue (Wright et al. 2004). Protective tissues, such as epidermis and fibres, tended to increase leaf biomass. Thus, a low value of SLA would translate into more resistant leaves to grazing and mechanical damage, with consequent relatively larger leaf life span and slow-return of initial energy investment in the leaf (Wright et al. 2004; Poorter et al. 2009). In contrast, high SLA means fast-return of energy investment, which would result in higher rates of net photosynthesis (Reich et al. 1997), potential growth (Grime et al. 1997) and transpiration (Reich et al. 1999). The fast-return of energy investment represented the main biological reason for the correlation between SLA and hydrologic reinforcement (Fig. 9), because of the different transpiration rates (Fig. 3) in agreement with Reich et al. (1999). Under European temperate climate condition, deciduous species are generally characterized by high SLA and hence a faster return of energy investment and transpiration during summer growing season (Bai et al. 2015). A recent study by Bochet and García-Fayos (2015) showed that SLA was a relevant trait for indicating plant competitiveness and the establishment success on road embankments in semi-arid environment. Thus, SLA, whose measurement is relatively simple and quick, appears to be a useful plant screening trait that could be

used to assess the relative hydrologic reinforcement and survival under the harsh environment of engineered slopes.

Among the below-ground traits, root length density (RLD) showed a significant correlation with matric suction and soil strength (Fig. 10). The effect of RLD on soil water depletion by plants has been reported in various agricultural (Yu et al. 2007; Nakhforoosh et al. 2014) and ecological (Pfeiffer and Gorchov 2015) studies. From the perspective of soil bioengineering, Osman and Barakbah (2006, 2011) identified RLD as a relevant trait for both the mechanical and hydrologic reinforcement to the soil. They found that RLD was positively correlated with soil shear strength, whereas it was negatively related to soil water content. In terms of the mechanical reinforcement, high RLD means a higher cross-section area of roots crossing a potential shear surface per unit of soil surface area (Ghestem et al. 2014a). However, as far as hydrologic reinforcement in deep soil is concern, RLD alone may not be sufficient to explain the amount of soil water depletion by a plant, although a significant correlation was found (Fig. 10). Other factors that could affect plant water uptake include a combination of other root traits such as the maximum root depth and specific root-water uptake (Hamblin and Tennant 1987). Moreover, a recent study carried out by Veylon et al. (2015) suggested that plants with high RLD would potentially induce fragmentation and remoulding in fine-grained soil, resulting in breakage of micro-pore network and hence the possibility of suppressing the development of matric suction.

Plant water uptake, and hence hydrologic reinforcement, is not exclusively related to the above- or the below-ground traits. Root:shoot ratio showed the best correlation with matric suction (Fig. 11a) and soil strength (Fig. 11b), when compared to other traits. This highlights the importance of considering the combined effects of both the below- and above-ground organs on the hydrologic reinforcement to soil. However, results from *C. scoparius* and *U. europaeus* did not fall in the linear regression. It is hypothesised that the outstanding behaviour of these two species may result from their distinct photosynthetic twigs and thorns, compared with the other eight species. Although the photosynthetic organs, mainly twigs and thorns, of these two outstanding species are photosynthetically analogues to leaves, they have greater mass per surface area. Thus, *C. scoparius* and *U. europaeus* may require greater above-ground biomass investment

to obtain the same photosynthetic active surface of broad-leaf species (i.e., the other eight species), hence resulting in much higher shoot weight (i.e., low root:shoot ratio).

Plant water uptake is the result of the eco-physiological interactions between the below- and above-ground processes. Roots contribute to the overall plant water-demand, and they also account for 50% to 60% of the hydraulic resistance of the entire plant, which substantially limits the water transport in the soil-plant-air continuum (Tyree and Ewers 1991). Plant shoot, when referring to leaves and stomata, controls and regulates plant water relations because of the steep gradient in water potential between a leaf and the atmosphere at the soil-plant-air water continuum (Steudle 2001; Jones 2013). Although both roots and shoots are important to water uptake, our results (Fig. 11) show that an increase in root:shoot ratio could increase hydrologic reinforcement. Root:shoot ratio may also be a relevant trait for mechanical reinforcement. Indeed a higher root:shoot ratio means that there is a relatively large number of roots potentially contributing to mechanical soil reinforcement, whilst the above-ground biomass is relatively small, inducing less surcharge and wind loading (Stokes et al. 2008) or seismic loading (Liang et al. 2015).

Conclusions

This study quantified and compared the transpiration-induced suction, and its effects on the change in soil strength, for ten selected woody species widespread in Europe. The tested species showed significant differences in their effectiveness to induce soil matric suction. Deciduous species exhibited double the transpiration efficiency and leaf conductance to water vapor of evergreen species. We identified that plant traits including specific leaf area, root length density and the root:shoot ratio showed significant and positive correlations with transpiration-induced suction. These traits therefore may be used as plant screening/selection criteria relevant to soil hydrologic reinforcement. We did not find any correlation between biomass and transpiration-induced suction, indicating that transpiration-induced suction was influenced more by other physiological factors, such as leaf conductance and biomass allocation. In particular, the effect of biomass allocation was

highlighted by the positive correlation between root:shoot ratio and hydrologic reinforcement.

This study focused on the hydrologic responses of vegetated soils during early stage establishment period. Future work is needed to study the changes in plant traits over time and how these changes affect the soil hydrologic reinforcement. The relative efficiency of root water uptake by deciduous and evergreen species in fostering hydrologic reinforcement should be further investigated for longer period of time over several growing seasons.

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